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Object Priming in the Fusiform Cortex: Exploring Effects of Task and Visual Similarity

by

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ABSTRACT

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Neural priming for same and different exemplars and viewpoints of objects was examined in two experiments using functional magnetic resonance imaging. In line with previous studies, viewpoint- and exemplar-specific priming was observed in the right fusiform gyrus (RFG). In contrast to some studies, viewpoint- but not exemplar-abstract priming was observed in the left fusiform gyrus (LFG). In the first experiment, neither task-demands nor visual similarity affected priming in the LFG. However, the RFG, including an area specialized for processing faces (the fusiform face area) was sensitive to the visual similarity of exemplar pairs. The second experiment explored this unpredicted result, but did not replicate the visual similarity effects. Results suggest that RFG and LFG are differentially sensitive to changes in viewpoint and are unaffected by task demands or visual similarity.

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I would like to thank all of my committee members for their continual support and guidance. The completion of this thesis would not have been possible without all of their help. I would also like to thank my friends and family for their never-ending support. Their financial and social support has contributed to the success of my studies.

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Object Priming in the Fusiform Cortex: Exploring Effects of Task and Visual Similarity

One of the more interesting aspects of the visual system is that an individual can accurately identify a wide array of visual input forms despite the lack of uniform appearance. Although two cups may have entirely different physical properties, it is still possible to identify both as cups, while also distinguishing one particular cup from another. Similarly, the cup can be recognized even if viewed from different viewpoints, regardless of whether or not the viewpoint produces a similar input image as to that viewed typically. The visual system processes stimuli in such a way that one can recognize different exemplars and viewpoints of an object as belonging to the same, abstract category, but that they each belong to different, specific categories defined by their form. According to the recognition-by-components (RBC) model of object recognition, the visual system achieves both specific and abstract forms of object recognition through the use of a perceptual mechanism that derives the basic components, or geons, of objects, and arranges them to access object representations stored in memory. In other words, geons comprising different viewpoints and different exemplars of objects tend to overlap such that the abstract recognition of these varying visual input forms can be recovered; however, the specific recognition of an object relies on the direct match of geon configuration (Biederman, 1987; Hummel & Biederman, 1992). While this model provides an explanation of how the visual system can overcome problems of both specific and abstract recognition of objects, it remains unclear whether or not different areas of the brain mediate these two processes.

The dissociable subsystems theory of object recognition posits that separable neural networks support specific-object recognition, the identification of an object based

on its specific form, and abstract-object recognition, the identification of two objects being the same despite dissimilar appearances. In accordance with this theory, the right hemisphere supports specific-object recognition for both different viewpoints and exemplars of objects, whereas the left hemisphere supports abstract-object recognition for both different viewpoints and exemplars of objects (Marsolek, 1999; Burgund & Marsolek, 2000). That is, the theory suggests that the same left hemispheric networks mediate abstract recognition for both different viewpoints and exemplars of an object. However, the theory is based on findings from divided visual field studies, and thus can only be certain of hemispheric asymmetries concerning the two types of object recognition, but cannot definitively claim that the same anatomical region mediates recognition for different viewpoints and exemplars. Indeed, neuroimaging studies have investigated the role of the fusiform cortex, an area consistently activated during object recognition, in the separable neural networks recruited for specific and abstract object recognition (Koutstaal et al., 2001; Simons, Koutstaal, Prince, Wagner, Schacter, 2003; Vuilleumier, Henson, Driver, & Dolan, 2002). While there is no dispute over the finding that the right fusiform gyrus (RFG) mediates specific visual form processing, the extent to which the left fusiform gyrus (LFG) mediates abstract visual form processing remains unclear. In particular, some neuroimaging studies suggest that the LFG stores different exemplars of an object in an abstract manner (Koutstaal et al., 2001; Simons et al., 2003), while another implicates this region in storing different viewpoints, but not exemplars, of an object in an abstract manner (Vuilleumier et al., 2002). In the present experiment, we aimed to replicate previous findings in regards to specific- and abstract-viewpoint

recognition, and investigate factors that possibly affect specific- and abstract-exemplar recognition, such as task and exemplar pair visual similarity.

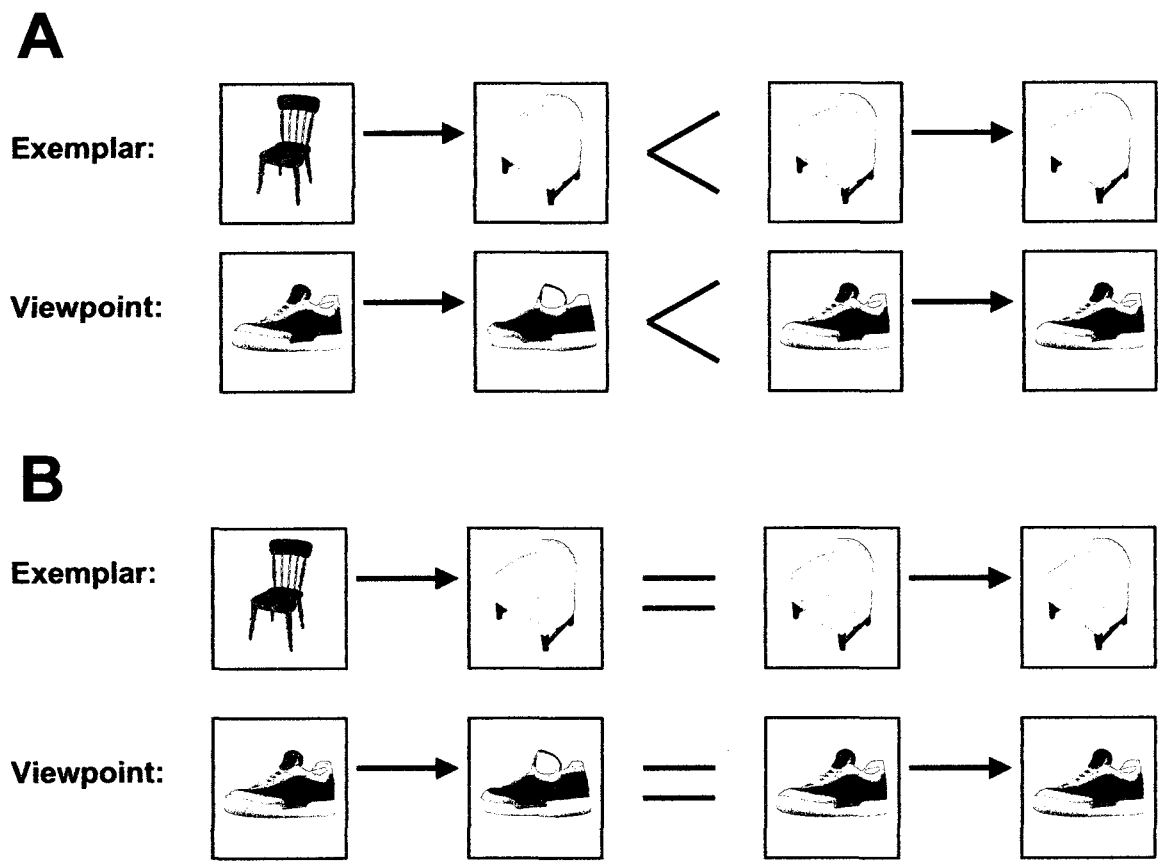

Figure 1. Illustration of both specific and abstract priming for different viewpoints and exemplars of objects. Specific-priming is evidenced when the priming magnitude for different-primed objects is less than that for same-primed objects (A). Abstract priming is evidenced when the priming magnitude for different- and same-primed objects does not differ (B).

Support for specific- and abstract- object recognition has been obtained in previous studies of object priming. Specific-object recognition is evidenced by greater same viewpoint or exemplar than different viewpoint or exemplar priming. Abstract-object recognition is evidenced when test objects are processed equally well after having viewed an object of a different viewpoint or exemplar than during initial encoding. For the purposes of this paper, the four types of object priming that will be described are as

follows: viewpoint-specific priming, viewpoint-abstract priming, exemplar-specific priming, and exemplar-abstract priming (see Figure 1).

Object-specific priming has been observed in divided visual field studies when objects of the same viewpoint or exemplar are presented to the right hemisphere. In contrast, object-abstract priming has been observed in divided visual field studies when different viewpoints of the same object or different exemplars of an object are presented to the left hemisphere. That is, the findings from such studies implicate the right hemisphere's involvement in viewpoint - and exemplar-specific recognition and the left hemisphere in viewpoint- and exemplar-abstract recognition. Because of these hemispheric asymmetries, it has been suggested that a specific visual-form (SVF) subsystem operates more effectively in the right hemisphere than the left, and an abstract visual-form (AVF) subsystem operates more effectively in the left hemisphere than the right (Marsolek, 1999; Burgund & Marsolek, 2000). Since behavioral experiments indicate distinctly lateralized sub-systems involved in object recognition, neuroimaging studies have investigated these hemispheric asymmetries in areas of the brain known to be involved in object recognition.

One area of the brain consistently activated during object recognition is the lateral occipital complex (LOC; Malach et al., 1995; Grill-Spector, Kourtzi, & Kanwisher, 2001). Findings from divided visual field studies suggest that regions of the LOC located in the right hemisphere would support specific-object recognition, whereas those in the left hemisphere would support abstract-object recognition. Within the LOC, the fusiform cortex, which includes the right and left fusiform gyri, demonstrates involvement in the aforementioned paths to object recognition. Indeed, functional magnetic resonance

imaging (fMRI) studies examining the neuroanatomical correlates of specific- and abstract-object recognition have garnered support for the findings from divided visual field studies, demonstrating that specific recognition for viewpoints (Vuilleumier et al., 2002) and exemplars (Koutstaal et al., 2001; Simons et al., 2003; Vuilleumier et al., 2002) recruited the right fusiform gyrus (RFG), and abstract recognition for viewpoints (Vuilleumier et al., 2002) and exemplars (Koutstaal et al., 2001; Simons et al., 2003) recruited the left fusiform gyrus (LFG). Surprisingly, however, failure to find exemplar-abstract recognition in either the right or left fusiform gyrus has also been reported in the neuroimaging literature (Vuilleumier et al., 2002). It has been argued that these conflicting results are due to either methodological constraints of the experiment and/or an artifact of the stimuli employed. That is, some suggest this divergent finding may reflect a lack of exemplar pair name agreement (Simons et al., 2003) and/or that the pairs may have been too visually dissimilar (Simons et al., 2003; Vuilleumier et al., 2002). The RBC model of object recognition does posit that exemplars with a common name are more likely to share geons, and the extent to which different exemplars prime one another depends on the overlap between both study and test geons. Thus, according to this model, visually dissimilar exemplar pairs may lack common basic visual components necessary for priming (Biederman, 1987; Hummel & Biederman, 1992). However, it has also been shown that the subsystems recruited for the recognition of an object are largely dependent on the demands of the task at hand (Burgund & Marsolek, 1997; Marsolek & Hudson, 1999; Large, Aldcroft, & Villis, 2007; Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006; Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997; Gauthier et al., 2002).

One can imagine that if asked to identify an eagle rather than bird, specific object recognition would be required for the former and abstract object recognition for the latter.

Divided visual field studies have observed task-dependent effects of specific- and abstract-object recognition. In a letter-case priming study conducted by Burgund and Marsolek (1997), the researchers found that subjects instructed simply to perceptually identify previously viewed letter strings did not demonstrate a right hemisphere advantage for case-specific priming. However, altering the task demands so that subjects were required to identify the previously viewed letter strings in the same case as initial encoding resulted in case-specific priming in the right hemisphere, providing evidence that SVF subsystems operate more effectively in the right hemisphere, but that the efficiency of this subsystem is dependent on the task. Therefore, it is possible that the recruitment of SVF and AVF subsystems depends on the task performed while viewing objects. In the aforementioned neuroimaging experiments, the researchers who found exemplar-abstract recognition in the LFG (Koutstaal et al., 2001; Simons et al., 2003) utilized a different task from those who did not (Vuilleumier et al., 2002), which, in turn, could have affected the extent to which different exemplars of an object recruited an AVF subsystem mediated by the LFG.

In fMRI experiments, priming is evidenced by a reduction in neuronal activity associated with processing a primed (repeated) compared to an unprimed (unrepeated) stimulus (Buckner et al., 1995, 1998; Maccotta & Buckner, 2004; Schacter & Buckner, 1998; but see Henson, Shallice, & Dolan, 2000; Turk-Browne, Yi, Leber, & Chun, 2007), and may be more sensitive to differences between stimulus types than estimates of overall activity (Grill-Spector & Malach, 2001). Therefore, in order to detect differential

activity between each prime type, the following experiments discussed here implemented an object-priming paradigm in which the activation for same, different viewpoint, or different exemplar primed objects is compared with that of activation for unprimed objects; however, as previously mentioned, these experiments utilized different tasks to assess these priming effects.

Support for the role of SVF and AVF subsystems in the right and left hemispheres, respectively, comes from studies examining the neuroanatomical correlates of priming for different exemplars of objects through the use of a size-judgment task. In this task, subjects are presented with pictures of objects, and instructed to decide whether the referent of each object is larger or smaller than a 13-inch square box. In the experiments of interest, the researchers presented an actual 13-inch square box to the subjects in order to provide a concrete frame of reference for making this judgment. While in the scanner, subjects performed the same task during the initial encoding phase and subsequent test phase, in which the objects were presented several times during encoding. As previously mentioned, the researchers found reduced neuronal activity in the RFG for same primed objects over different exemplar and unprimed objects, signifying object-specific recognition. In the LFG, reduced neuronal activity was found for different exemplar priming relative to unprimed objects when compared with the RFG, indicating this area supports abstract-object recognition (Koutstaal et al., 2001; Simons et al., 2003). These results support the dissociable subsystems theory in that a SVF subsystem operated more effectively in the right hemisphere and an AVF subsystem operated more effectively in the left hemisphere.

In contrast, a study in which subjects performed an object-decision task provides conflicting evidence against an AVF subsystem in the left hemisphere when recognizing objects across different exemplars. In an object-decision task, subjects are presented with images of real objects and non-objects, or nonsense objects, and the task is to decide whether or not the object is real. In this study, the authors not only investigated object recognition across exemplars (Experiment 1), but they also examined the recognition of an object from varying viewpoints (Experiment 2). In the first experiment, the different exemplars of objects were presented later in the same trial; whereas, in the second experiment, different viewpoints of objects from the first experiment were presented. In regards to exemplar priming, the results revealed decreased neuronal activity in the RFG for repeated presentations of the same object as compared to different exemplars and unprimed objects, as predicted. Yet, unexpectedly, the results did not demonstrate exemplar-abstract recognition in either right or left fusiform gyri, thus concluding that the RFG and LFG mediate exemplar specific, but not abstract, priming (Vuilleumier et al., 2002). While these results diverge from those previously obtained in regards to different exemplar priming (Marsolek, 1999; Koutstaal et al., 2001; Simons et al., 2003), findings from the second experiment investigating different viewpoint priming supports previous research (Burgund & Marsolek, 2000), in that the researchers found decreased neuronal activity for the repeated presentations of the same viewpoint in the RFG and for different viewpoints the LFG (Vuilleumier et al., 2002). Consequently, these findings complicate the interpretation of exemplar priming effects in the brain, and call to question the exact nature of SVF and AVF subsystems.

Some argue that failure to demonstrate exemplar-abstract recognition in the LFG might be due to differences in the names of the objects coupled as exemplar pairs, as Vuilleumier and colleagues (2002) did not report data on naming agreement. Moreover, it has also been suggested that the exemplar pairs used in Vuilleumier et al. (2002) may have been too visually dissimilar, which could also affect whether or not participants would consider the paired objects as the same object with a common name (Simons et al., 2003). Indeed, prior studies that observed exemplar-abstract priming did ascertain a measure of name agreement for exemplar pairs (Koutstaal et al., 2001; Simons et al., 2003), therefore it is possible that exemplar pair name agreement and/or visual similarity affected abstract priming; however, it is also counterintuitive to think that an AVF subsystem would rely on such bottom-up processes based on specific visual form in order to access the abstract representation of that object, unless of course, subjects did not consider the exemplar pairs as the same object. It could also be argued that the difference in findings for exemplar-abstract priming in the fusiform cortex is task-related, as previous research has found that this area is sensitive to task demands (Joseph et al., 2006; Gauthier et al., 2002; Large et al., 2007) and the recruitment of SVF and AVF subsystems is task dependent (Burgund & Marsolek, 1997; Marsolek & Hudson, 1999). The study that did not demonstrate exemplar abstract priming used a object-decision task, in which participants could be employing "lower-level" visual processes based on familiarity (Vuilleumier et al., 2002); whereas, experiments that did demonstrate this effect used a size-judgment task, where participants have to use "deeper-level" processing to perform the task accurately (Koutstaal et al., 2001; Simons et al., 2003). In other words, when asked to determine the size of an object, one must recall the object's

referent in real-life, which, in turn, may activate further knowledge of the object, such as its name and other visual representations of objects with the same name. Thus, the size-judgment task may prime other exemplars of the object by merely requiring that subjects think in depth about the properties of that object. In contrast, when asked to determine an object's existence in real-life, one can perform this task with great accuracy without having to retrieve prior knowledge of the object's referent in real-life. Therefore, it is possible that an AVF subsystem, operating more effectively in the left hemisphere, was not recruited for the object-decision task because performing this task does not call for processing abstract category membership information. This task would, however, involve the recruitment of a SVF subsystem in order to perceptually identify the visual form of the object as real or nonsensical.

Experiment 1

In this experiment, we investigated the effect of task-demands on fusiform cortex activation by having subjects perform either the object-decision task or the size-judgment task. The first aim of this study is to examine the patterns of activation for the different tasks when priming across exemplars. The present experiment will address the possible explanations for the divergent findings concerning exemplar abstract recognition (Koutstaal et al., 2001; Vuilleumier et al., 2002; Simons et al., 2003) by obtaining a measure of name agreement and exemplar pair similarity.

If priming for objects across different exemplars in the fusiform cortex is sensitive to task demands, it should follow that subjects performing the object-decision task demonstrate neural activity consistent with that of exemplar-specific, but not exemplar-abstract, priming in the right and left fusiform gyri. Yet, subjects performing the size-

judgment task should demonstrate neural activity consistent with that of exemplar-specific priming in the RFG and exemplar-abstract priming in the LFG. On the other hand, if exemplar-abstract priming in the LFG is not sensitive to task-demands, and failure to demonstrate abstract recognition across different exemplars was due to the lack of name agreement or visual similarity, the preliminary data acquired will be able to parse apart these issues. Because this experiment obtained a measure of name agreement across exemplars, differences in activation cannot be attributed to this argument. However, if LFG mediation of exemplar-abstract recognition is susceptible to visual similarity, in that visually dissimilar objects do not prime one another, then it is expected that exemplar-abstract priming will be observed only for visually similar exemplar pairs, and not for those rated as visually dissimilar.

This experiment also aims to replicate previously obtained viewpoint-priming effects, which suggest that viewpoint-specific priming recruits the RFG and viewpoint-abstract priming recruits the LFG (Vuilleumier et al., 2002; Experiment 2). At present, viewpoint recognition, both specific and abstract, has not been extensively investigated from a neurological perspective, and is in need of further exploration. In a study investigating the neural substrates of mental rotation and object recognition, Gauthier and colleagues (2002) observe viewpoint-dependent, or specific, recognition in the RFG, but not viewpoint-independent, or abstract, recognition in the LFG. The findings from this study will provide further insight in regards to the hemispheric asymmetries associated with viewpoint priming effects.

Additionally, the present experiment seeks to explore whether or not the recognition of objects recruits an area within the RFG known as the "fusiform face area"

(FFA) that, in some studies, shows selective activation for the recognition of faces over other classes of objects (Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Kanwisher, Tong, & Nakayama, 1998; Yovel & Kanwisher, 2004; Loffler, Yourganov, Wilkinson, & Wilson, 2005). These experiments implicate a domain-specific function of the FFA in face processing. However, others have found FFA activation for other classes of objects, suggesting that this region is not necessarily a face-specific processing area (Haxby et al., 2001), but instead a generic object recognition system that is recruited when the perceptual demands of the object are similar to those of faces (Tarr & Gauthier, 2000; Gauthier et al., 1997; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gauthier, Skudlarski, Core, & Anderson, 2000; Gauthier et al., 2000). The domain-general hypothesis, or the idea that the FFA is process-specific and not stimulus-specific, is supported by a number of studies demonstrating that the representation of faces in the brain overlaps with that of objects (Haxby et al., 2001), and that the recruitment of this area depends on one's perceptual expertise with the object class. Based on these findings, some researchers suggest that the FFA supports subordinate level recognition automated by expertise, and faces are one such class of objects that everyone has expertise with recognizing. In other words, faces and, in some cases, objects demand holistic and configural processing, which are characteristics of subordinate level processing (Gauthier et al., 2000; Tarr & Gauthier, 2000; Gauthier et al., 1999). Therefore, we hypothesize that the FFA could also support specific-object recognition, as evidenced by specific priming for both different viewpoints and exemplars, if this area is process-specific and not face-specific. To test this idea, the present study incorporated an additional task—one designed to identify the FFA.

Accordingly, if the FFA supports viewpoint- and exemplar-specific priming, this priming should be observed in the area defined based on the FFA localizer task.

Method

Design.

A 2 x 4 x 2 mixed factorial design was employed in which task (object-decision vs. size judgment) was a between-subjects variable and prime type (unprimed vs. same vs. different-viewpoint vs. different-exemplar) and visual similarity (similar vs. dissimilar) were the within subjects variables. For an example of each prime type, see Figure 2.

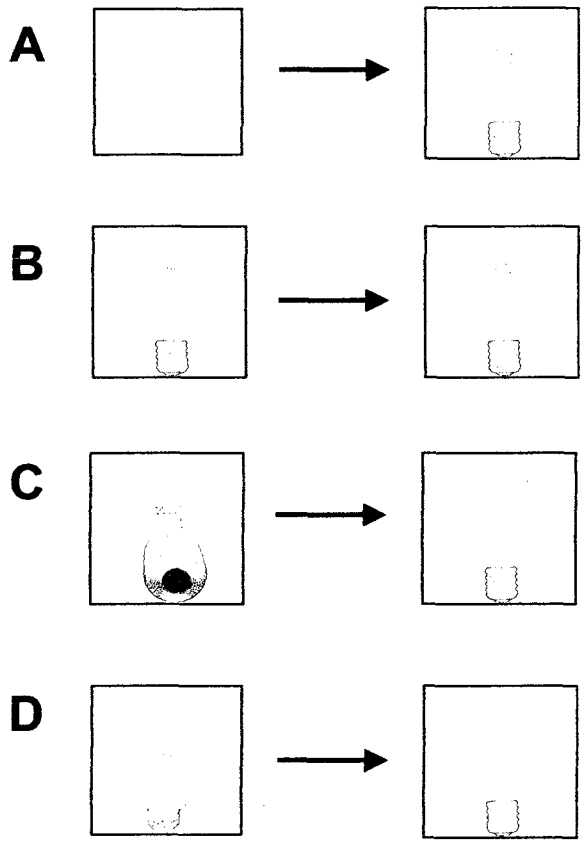

Figure 2. Examples of the four prime types: unprimed (A), same (B), different viewpoint (C), and different exemplar (D). The left column represents what subjects see during the encoding phase, and the right column represents what subjects see during the test phase.

Subjects.

Twenty volunteers (10 male; mean age 21) from Rice University and Baylor College of Medicine participated in the fMRI study. All subjects completed a screening questionnaire to ensure they had no history of neurological or psychiatric problems. Additionally, all subjects were right-handed, and had normal, or corrected-to-normal, vision. Informed consent was received from each participant in adherence to the guidelines and endorsement of the Institutional Review Board at Rice University. Subjects were paid for their participation.

Materials.

Stimuli were images of 80 objects selected from the Verfaillie and Boutsen (1995) corpus of depth-rotated images of familiar objects and from the corpus provided by Michael J. Tarr, Brown University (http://www.tarrlab.org/). These objects were named and rated in a normative behavioral study, in which 29 Rice University undergraduate students received course-credit in their psychology classes for their participation. Each subject was required to indicate their native language and the order in which they learned additional languages, if any. Informed consent was received from each participant, and upon completion of the experiment, subjects were given a debriefing form explaining the purpose of the experiment.

Subjects received three different packets designed to evaluate exemplar pair name agreement and visual similarity as well as object viewpoint typicality. The naming packet was always given first, and the similarity and typicality rating packets were completed either second or third. In the naming packet, a blank space and the letters "B" for "Bigger" and "S" for "Smaller" appeared underneath each image, and subjects

indicated the name of the object and whether or not its referent in real-life is bigger or smaller than a 13-inch box. For this judgment, subjects could refer to a 13-inch box drawn on the chalkboard. For the similarity and typicality rating packets, rating scales appeared under each exemplar pair situated next to one another or a single object, and subjects were to rate the visually similarity of each pair or how typical it would be to see the object from that viewpoint, respectively. Ratings were from one, very dissimilar or atypical, to six, very similar or typical. For these ratings, subjects were instructed to distribute their responses across all six points rather than always respond with a one or a six. In both the naming and viewpoint typicality package, no two exemplar pairs appeared on the same page.

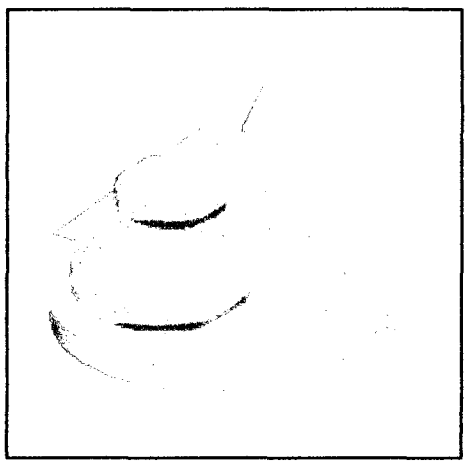

Figure 3. Example of a nonobject used for the purposes of the object-decision task.

Based on the results from the behavioral experiment, 20 objects were later omitted from the fMRI portion of the experiment for obtaining less than 90 percent name agreement among the raters in the normative behavioral study. A median split of the objects based on the visual similarity ratings determined pairs considered as visually similar and dissimilar, which were later used to analyze the imaging data. Typicality

ratings were used for counterbalancing purposes only. Thus, a total of 60 real objects with 30 similar exemplar pairs and 30 dissimilar pairs were included in the fMRI experiment. Thirty nonobjects, selected from Burgund (2000), were included for the purpose of the object decision task (see Figure 3). For each of the real objects, two views and one different exemplar of the object were selected (Figure 4). The different views for each object varied in that the different-viewpoint image was rotated in depth by 45, 60, 90, 75, or 105 degrees from the original presentation. The 60 objects were divided into four lists, with each list containing 15 objects. The lists were counterbalanced on all the measures rated in the normative data (exemplar similarity, viewpoint typicality, and size) so that each list obtained an equal number of similar exemplar pairs, typical viewpoints, and objects that were smaller or larger than a 13-inch box (see procedure below). The degree to which each object rotated from its original presentation was counterbalanced across lists as well.

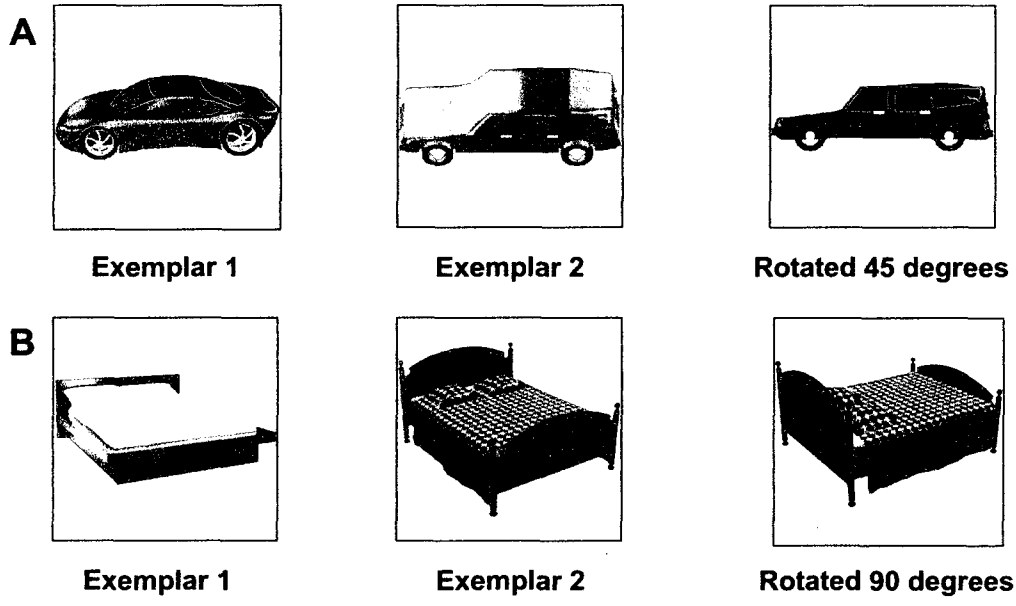

Figure 4. Example of an exemplar pair and a different viewpoint rotated 45 degrees (A). Example of an exemplar pair and a different viewpoint rotated 90 degrees (B).

For the FFA localizer task, images of 26 faces were selected from the corpus provided by Michael J. Tarr, Brown University (http://www.tarrlab.org/), and images of 26 houses were selected from an online source (http://www.turbosquid.com/). The faces selected depicted a neutral mood, and comprised of different ethnicities representative of the population. All the houses were presented from the same viewpoint and did not contain extra visual distracters, such as grass, plants, or trees (see Figure 5).

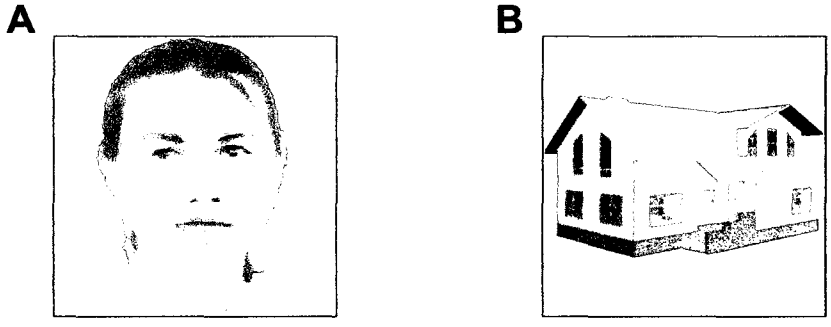

Figure 5. Example of a face (A) and house (B) that were used for the FFA localizer task.

All images were presented centrally, in grayscale against a white background, and subtended approximately 2° x 2° of visual angle. Presentations and response-time measurement were controlled by the PsyScope software package (Cohen, MacWhinney, Flatt, & Provost, 1993).

Procedure.

The images were presented for 1000 ms during the encoding phase and 500 ms for all other trials at intervals 2.5 s, 5 s. or 7.5 s (average rate of 1 image per 5 s). A fixation cross (+) preceded each presentation and remained on the screen between stimulus trials. During the encoding phase, subjects were instructed to rate how frequently they encounter each object in their everyday life, using a four-point scale that corresponded to the four keys located on the response box. For the encoding trials,

subjects were asked to make their response after each object disappeared from the screen. In the object-decision task, subjects were instructed to decide whether the object presented was a real object or a nonobject. In the size-judgment task, subjects were first shown an actual 13-inch square box before entering the scanner, and once in the scanner, subjects determined whether the object presented was larger or smaller than the 13-inch square box. The stimulus presentations remained the same regardless of task; therefore, subjects performing the size-judgment task were asked to withhold their response when a nonobject appeared on the screen. That is, subjects performing this task were instructed not to press a key when presented with a nonobject. In the testing phase, subjects were asked to respond as quickly and accurately as possible by pushing a button with their left (or right) hand to indicate the "object" or "bigger" response and a button with their right (or left) hand to indicate the "nonobject" or "smaller" response. The response hand was counterbalanced across subjects. During the FFA localizer task, subjects were presented with either a face or a house and instructed to watch each image presented on the screen, and then press a button on each of the response boxes at the same time as soon as it disappears from the screen.

Subjects completed two runs of the encoding phase, in which they saw each object twice. After completion of the encoding task, subjects were then given instructions on the testing task (either object-decision or size-judgment), and completed two runs of the assigned task. Each of the test items were split into two trials, in which the nonobjects and unprimed objects were presented intermixed with either the same, a different viewpoint, or different exemplar of the objects presented in the encoding run. Lastly, subjects completed two runs of the localizer task. In each run, no more than three

runs of the same prime type (unprimed vs. same vs. different-viewpoint vs. different-exemplar) or stimulus type (object vs. nonobject; face vs. house) appeared consecutively. The encoding runs lasted approximately six minutes, the testing runs lasted approximately five minutes, and the localizer runs lasted approximately three minutes.

Image Acquisition.

fMRI data was collected at the Human Neuroimaging Laboratory at Baylor College of Medicine. At the start of each scanning run, a 10s fixation period occurred to allow for stability of magnetization. At the end of each scanning run, a 15s fixation period occurred to compensate for the delay in hemodynamic response.

Structural and functional magnetic resonance images were acquired on a Siemens 3T Allegra scanner (Erlangen, Germany). Anatomical images were acquired first, using a transverse MP-RAGE T1-weighted sequence (Siemens) with a voxel size of .5 x .5 x 1 mm (TR = 1200 ms; TE = 2.93 ms; flip angle = 12°). Functional images were acquired using an echo-planar sequence (TR = 2500 ms; TE = 40 ms; flip angle = 90°). During each functional run, 108 (encoding phase), 131 (testing phase), and 62 (localizer phases) sets of 26 contiguous 4-mm thick axial images were acquired parallel to the anterior-posterior commissure plane.

Image Analysis.

Data from each subject were preprocessed to remove noise and artifacts, including correction for movement within and across runs using a rigid-body rotation and translation algorithm (Friston, Jezzard, & Turner, 1994; Snyder, 1996). Image slices were temporally realigned (using sinc interpolation) to the midpoint of the first slice, accounting for differences in the acquisition time for each individual slice. Data were

then resampled into 2-mm isotropic voxels and warped into a standardized atlas space (Talairach & Tournoux, 1988).

Preprocessed data were analyzed using the General Linear Model (GLM; Friston et al., 1994; Josephs, Turner, & Friston, 1997; Miezen, Maccotta, Ollinger, Peterson, & Buckner, 2000; Zarahn, Aguirre, & D'Esposito, 1997) in the FIDL analysis package (http://www.nil.wustl.edu/~fidl). No shape was assumed for the priming effects. Instead, neural signals throughout the eight conditions of interest [prime type (4); similarity (2)] to assess priming effects and for the two conditions of interest [faces vs. houses] to localize the FFA were modeled in the GLM across the seven time points (i.e., image acquisitions), beginning immediately after the onset of stimuli. Additionally, a factor was coded in order to account for the within-run linear trend (linear drift and a constant term). All effects were modeled concurrently in the GLM for each participant.

Regions exhibiting object priming effects and those localizing the FFA were defined based on two separate voxel-wise analyses. In order to identify regions demonstrating object-priming effects, a two-way, repeated measures ANOVA was performed, in which time (at seven time points) and prime type (same primed vs. unprimed) were the independent variables. The *F* statistical image produced by this analysis was smoothed by a 2-mm radius hard sphere kernel. Regions of interest corresponding to the FFA localizer task were defined based on a two-way, repeated-measures ANOVA, in which time (at the seven time points) and stimulus type (face vs. house) were the independent variables. The statistical image for the localizer was smoothed by a 4-mm radius hard sphere kernel. Each of the statistical images were masked by an additional image reflecting voxels in which the percent change in bold

signal from baseline differed for same-primed compared with unprimed objects (object priming effects) or faces compared with houses (FFA localizer). Thereafter, a peak (local extremum) search algorithm was used to identify the coordinates (Talairach and Tournoux, 1988) of activation peaks ($P < .002$, uncorrected) in the masked images. In each image, coordinate averaging combined peaks separated by less than 10-mm, and spheres (10-mm radius) were centered on each peak. Finally, spherical regions were masked to exclude voxels that did not reach a statistical threshold of $P < .001$ (uncorrected).

Region-based analyses were conducted on those regions identified in the voxel-wise analyses. Object priming effects were assessed in a mixed factorial ANOVA in which time (at the seven time points) and prime type (same vs. different viewpoint vs. different exemplar vs. unprimed) and similarity (similar vs. dissimilar) were the within-subject independent variables and task (object-decision vs. size-judgment) was the between-subject independent variables. The FFA was localized using a two-way, repeated measures ANOVA in which time (at the seven time points) and stimulus type (face vs. house) were the independent variables.

Results

Effect of Prime Type.

Two regions within the fusiform cortex emerged from the voxel-wise ANOVA assessing object priming effects (Figure 6). Importantly, these regions were centered on coordinates in stereotactic space in the left fusiform gyrus (-48, -63, -11 [Figure 6A]) and the right fusiform gyrus (35, -55, -18 [Figure 6B]; Talairach & Tournoux, 1988) that were close to those found in previous studies exploring object priming effects (-40, -52, -

6 and 46, -58, -6; Koutstaal et al., 2001; -45, -60, -18 and 42, -57, -18; Vuilleumier et al., 2002; -45, -54, -24 and 48, -66, -15; Simons et al., 2003). Analyses of prime type were conducted with a *t*-test comparing activity for the different prime types averaging across the third and fourth time points (5-7.5-s post stimulus onset; i.e. the peak of the typical hemodynamic response function). This averaging assumes that meaningful differences between prime-types are observed at the peak of the response function.

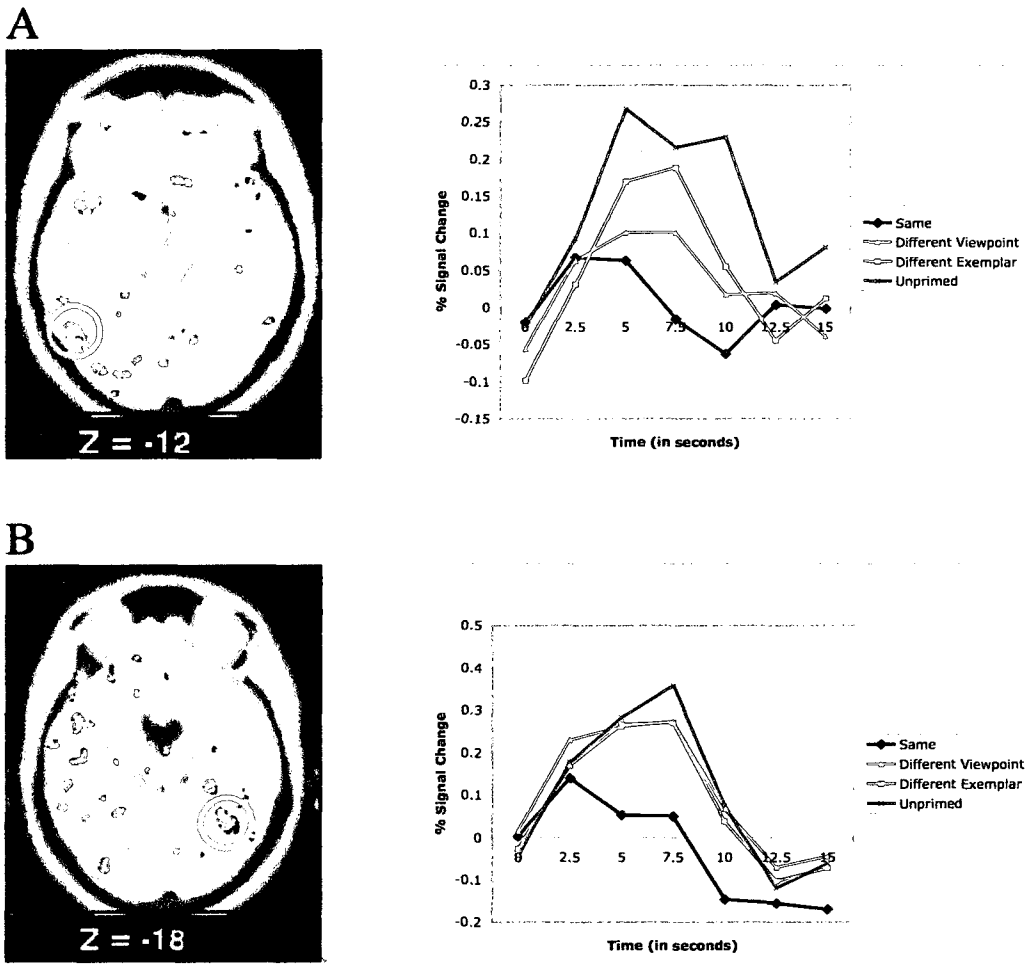

Figure 6. Regions exhibiting neural priming effects in the fusiform cortex when collapsed across task and visual similarity: the left fusiform gyrus (A [-48, -63, -11]) mediated viewpoint-abstract and exemplar-specific priming; and the right fusiform gyrus (B [35, -55, -18]) mediated both viewpoint- and exemplar-specific priming.

In the LFG, analysis of the peak activity for different-viewpoint primed objects revealed greater percent signal change for unprimed objects (.24) than for different viewpoints of objects (.10), $t(19) = -2.86$, $P < .02$. Moreover, the peak of the response for different viewpoint priming (.10) as compared with same primed objects (.02) is not statistically significant, $t(19) = -1.15$, $P > .26$, consistent with viewpoint-abstract priming effects in this region. When the peak of the response for different exemplars (.18) is compared with that of unprimed objects (.24), the magnitude of activation does not significantly differ, $t(19) = -1.33$, $P > .20$; however, activation for different exemplars does significantly differ from that of same primed objects, $t(19) = -2.31$, $P < .05$, thus exhibiting exemplar-specific priming in this region (Figure 7A). The difference in activation patterns for different viewpoint (.10) and different exemplar (.18) primed objects approached significance, $t(19) = 1.79$, $P = .09$, further suggesting that the LFG responds differently to these prime types.

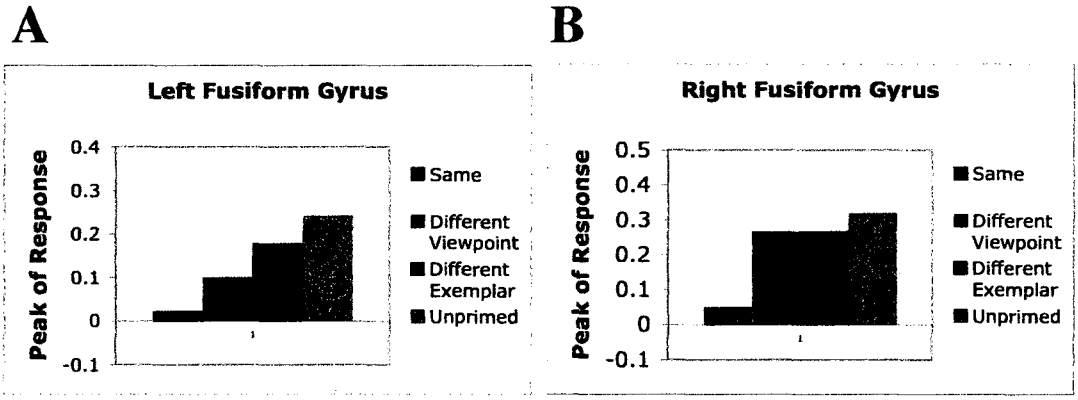

Figure 7. Peak of the hemodynamic response for prime types in the LFG (A) demonstrating viewpoint-abstract and exemplar-specific priming, and in the RFG (B) demonstrating viewpoint- and exemplar-specific priming.

Analyses of prime type in the RFG, revealed that the percent signal change for different viewpoints (.27) and different exemplars (.27) was greater than that for same-primed objects (.005), $t(19) = -3.53$, $P < .005$ and $t(19) = -5.40$, $P < .001$, but not

significantly different from unprimed objects (.32), $t(19) = -1.07$, $P > .29$ and $t(19) = -1.11$, $P > .28$ (Figure 7B). Taken together, these results demonstrate that the LFG mediates viewpoint-abstract and exemplar-specific priming, and the RFG mediates viewpoint- and exemplar-specific priming.

Effect of Task.

Analyses of task effects were assessed in the LFG and RFG via a two-way, mixed factorial analysis of variance comparing activity averaged across the third and fourth time points. In the LFG, this analysis revealed that the interaction between prime type (same vs. different exemplar) and task (object-decision vs. size-judgment) was not significant, $F(1, 18) = .03$, $P > .87$, nor was the interaction significant when comparing different-exemplar with unprimed objects, $F(1, 18) = .67$, $P > .42$. Similarly, in the RFG, the interaction between prime type (same vs. different-exemplar) and task (object-decision vs. size-judgment) was not significant, $F(1, 18) = .45$, $P > .51$, nor was it when the different exemplar and unprimed objects were compared, $F(1, 18) = .36$, $P > .55$.

Effect of Visual Similarity.

A median split of the similarity ratings obtained in the preliminary data collection determined visual similarity. The mean ratings obtained for those exemplar pairs considered similar (3.31) significantly differed from that of exemplar pairs considered dissimilar (4.77), $t(29) = 31.41$, $P < .0001$ (see Figure 8).

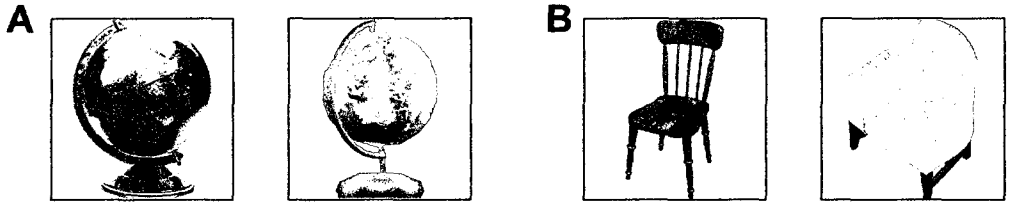

Figure 8. Example of an exemplar pair rated as visually similar (A) and visually dissimilar (B).

Analyses of exemplar pair similarity in both the LFG and RFG were assessed via a two-way, repeated-measures analysis of variance comparing activity averaged across the third and fourth time points. In the LFG, when exemplars are separated by visual similarity, no interaction between prime type (same vs. different exemplar) and visual similarity (similar vs. dissimilar) exists, $F(1, 19) = .89, P > .35$. In contrast, the analysis in the RFG revealed that there is a significant interaction between prime type (same vs. different exemplar) and visual similarity (similar vs. dissimilar), $F(1, 19) = 4.55, P < .05$. Simple comparisons decomposing this interaction shows that the magnitude of the peak activation for different exemplar similar (.40) is significantly greater than that for different exemplar dissimilar (.13), $t(19) = 2.17, P < .05$. Moreover, the difference in activation for similar exemplars and same primed objects is significant, $t(19) = -3.95, P < .001$; whereas there is no significant difference between dissimilar exemplars and same primed objects, $t(19) = -.29, P > .77$ (see Figure 9).

Figure 9. Peak of the hemodynamic response for visually similar (A) compared with visually dissimilar (B) exemplars in the RFG. Greater activation for visually similar exemplar pairs indicates exemplar specific priming (A), whereas a decrease in activation for dissimilar exemplar pairs indicates exemplar abstract priming (B).

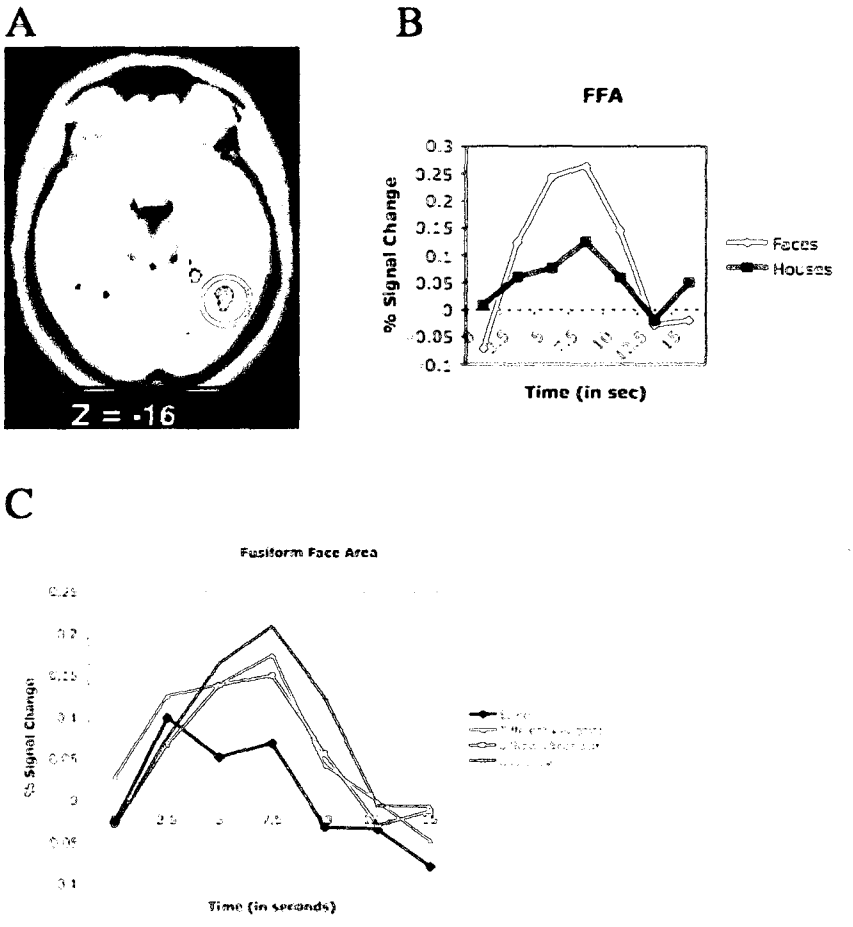

Figure 10. Region within the RFG localized as the FFA (A [41, -55, -15]) exhibiting greater activation for faces as compared to houses (B) and both viewpoint- and exemplar-specific priming (C).

FFA Localizer.

One region emerged from the voxel-wise analysis designed to anatomically localize the fusiform face area (FFA). Critically, the region was centered on coordinates in stereotactic space (41, -55, -18 [Figure 10A]; Talairach & Tournoux, 1988) in a region consistent with previous studies (Kanwisher et al., 1997; Loffler et al., 2005), and close to the RFG region obtained in the voxel-wise analysis comparing activation differences between same and unprimed objects over the seven time points (35, -55, -15). Region-based analysis revealed that this area within the RFG (41, -55, -18) shows greater peak activation for faces (.25) than houses (.10), $t(19) = 5.53$, $P < .0001$ (see Figure 10B),

which is characteristic of FFA activity. Analysis of objects in this area demonstrates a similar pattern of activation as found in the RFG region. First, it is important to note that this area mediates object priming, such that peak activation for same primed objects (.06) significantly differed for that of unprimed objects (.19), $t(19) = 3.10$, $P < .01$. Moreover, the pattern of activation for different viewpoints (.16) and different exemplars (.14) was greater than that for primed objects (.06), $t(19) = 2.59$, $P < .05$ and $t(19) = 1.93$, $P < .07$, implicating the role of this region for processing specific visual forms of object classes other than faces (Figure 10C).

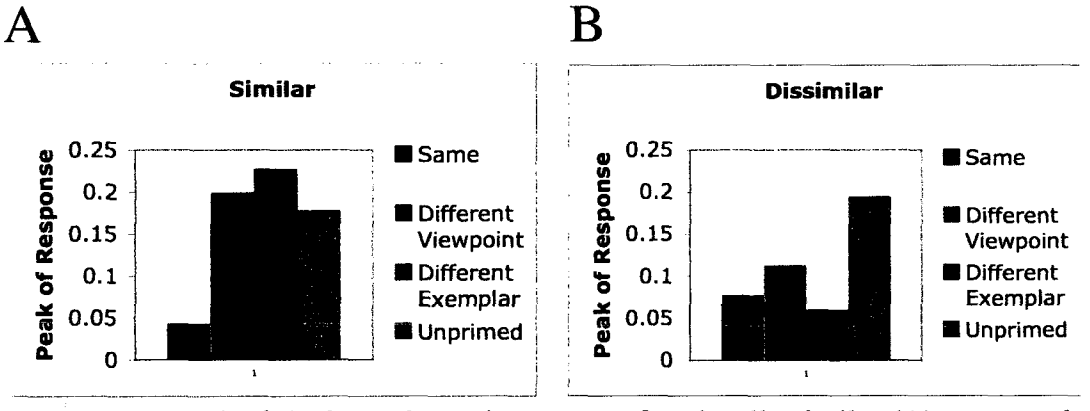

Figure 11. Peak of the hemodynamic response for visually similar (A) compared with visually dissimilar (B) exemplars in the FFA.

Effects of exemplar pair visual similarity were also assessed in the FFA, as patterns of activation in this region resembled that of the RFG, and the RFG demonstrated significant effects of this variable. A two-way, repeated-measures analysis of variance revealed that a significant interaction exists between prime type (same vs. different exemplar) and visual similarity (similar vs. dissimilar) in the region localized as the FFA, $F(1, 19) = 6.01$, $P < .05$. Accordingly, similar different exemplar primed objects (.23) exhibited greater activity than the dissimilar different exemplar primed objects (.06), $t(19) = 2.58$, $P < .02$. The percent signal change for similar different

exemplars as compared to same primed objects significantly differed, $t(19) = 2.64$, $P < .02$ (Figure 11A); on the other hand, activation for dissimilar different exemplars was not statistically different from that of same primed objects, $t(19) = -.37$, $P > .71$ (Figure 11B). Interestingly, the peak activation for faces (.25) did not differ from that of visually similar exemplar pairs (.23), $t(19) = .54$, $P > .59$. Likewise, the peak activation for houses (.10) did not differ from that of visually dissimilar exemplar pairs (.06), $t(19) = .55$, $P > .58$ (Figure 12).

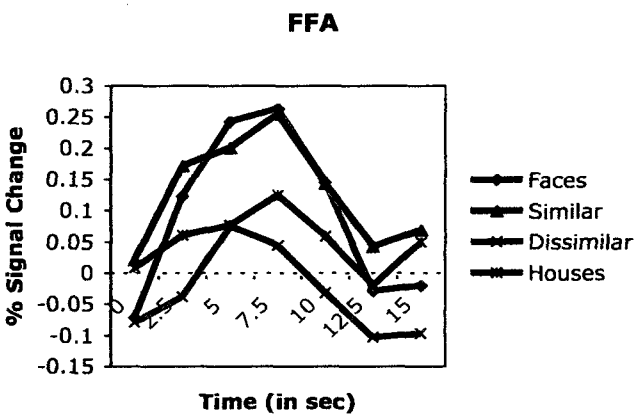

Figure 12. Within the FFA, activation patterns for visually similar and dissimilar exemplar pairs were analogous to those for faces and houses, respectively.

Discussion

In the present research, we investigated the effects of task demands and visual similarity on specific- and abstract-object recognition, in efforts to provide an explanation for differential findings of exemplar recognition obtained in previous neuroimaging experiments (Koutstaal et al., 2001; Vuilleumier et al., 2002; Simons et al., 2003), and to replicate earlier findings of viewpoint recognition (Vuilleumier et al., 2002). To address possible shortcomings of designs failing to find exemplar-abstract recognition, this experiment obtained measures of name agreement and visual similarity for each exemplar

pair. We hypothesized that the contradictory findings could reflect task-dependent effects, in which the levels of processing required by each task might affect the extent to which an object was represented abstractly. Contrary to what was predicted, results revealed that in both the left and right fusiform gyri, the task did not differentially affect priming magnitudes of different viewpoint or different exemplar primed objects, suggesting that this area is not sensitive to the demands of the tasks used. Therefore, the remainder of this discussion will focus on priming effects in the fusiform cortex when collapsed across task.

The analyses revealed two regions within the right and left fusiform gyri that demonstrated priming effects. Within these regions, we investigated the priming magnitude for different viewpoint and different exemplar primed objects. In line with previous findings, the results implicate the role of the LFG in storing objects in an viewpoint-abstract manner and the role of the RFG in storing objects in a viewpoint-specific manner (Vuilleumier et al., 2002). On the other hand, the results suggest that the RFG and LFG store objects in an exemplar-specific manner. Thus, in regards to both viewpoint and exemplar priming, these findings replicate those obtained by Vuilleumier and colleagues (2002), but contradict those implicating LFG involvement in exemplar-abstract recognition acquired in previous experiments (Koutstaal et al., 2001; Simons et al., 2003).

Some have argued that visually dissimilar exemplar pairs might not prime one another, specifically because the likelihood of such pairs sharing the same name decreases with visual similarity. Thus, previous results not demonstrating exemplar-abstract priming in LFG may reflect this methodological problem (Simons et al., 2003).

Unfortunately, exemplar pair naming agreement data was not reported in this study (Vuilleumier et al., 2002), therefore, it is difficult to assess whether or not the discrepant findings are due to one or both of these factors. In the present experiment, all exemplar pairs share a common name, but the extent to which pairs are visually similar varies. Results assessing whether or not visual similarity of exemplar pairs differentially affects abstract recognition in the LFG imply that this is not the case. Exemplar-specific priming was observed for both visually similar and dissimilar exemplar pairs when assessed in the LFG. Therefore, findings of exemplar-specific priming in LFG obtained in this study and a previous experiment (Vuilleumier et al., 2002) cannot be due to exemplar pair visual similarity.

While the recognition-by-components (RBC) model of object recognition posits that exemplar abstract recognition is achieved by matching similar geons from one exemplar to another (Biederman, 1987), experiments assessing this model imply that abstract recognition of different viewpoints of an object relies on somewhat different processes than that required for abstract recognition of different exemplars of an object (Biederman & Cooper, 1991; Biederman & Gerhardstein, 1993). In particular, Biederman and Cooper (1991) demonstrated that priming for contour-deleted images relied on whether or not the basic components, or geons, were present in both the initial encoding image and the complementary image shown at test; however, the magnitude of priming for contour-deleted different exemplar primed objects was less than that for complementary images of same primed objects, and did not depend on overlapping geons. The authors suggest that the different exemplar objects represent nonvisual benefits of name and concept priming. Similarly, another experiment comparing naming

latencies for different viewpoints and different exemplars of objects found that repeated presentations of different viewpoints of objects had a sizeable response time advantage over different exemplar primed objects. Moreover, the factor that affected the magnitude of priming was whether or not the geon structural descriptions could be recovered from each rotated image (Biederman & Gerhardstein, 1993). Taken together, these findings suggest that viewpoint abstract recognition is a bottom-up, visual process achieved by matching geon structural descriptions from one viewpoint of an object to a different viewpoint of that object. In contrast, exemplar abstract recognition represents top-down conceptual processes that rely heavily on stored knowledge of objects. Interestingly, an fMRI experiment provides evidence that the fusiform cortex represents geons of objects, rather than object concepts, as contour deleted same, but not different exemplar, primed images resulted in repetition suppression (Hayworth & Biederman, 2006). Thus, viewpoint abstract recognition relies on a different process than that required for exemplar abstract recognition, and the fusiform cortex appears to be sensitive to geon structural descriptions involved in the recognition of different viewpoints of an object, but not in the processing of abstract visual form information necessary for the recognition of different exemplars of objects.

What remains unclear is why other neuroimaging experiments demonstrate exemplar abstract recognition in the fusiform cortex (Koutstaal et al., 2001; Simons et al., 2003) if this area mediates processes by which visual, but not abstract visual form, priming occurs. It is possible that the previous demonstrations of exemplar-abstract priming effects in LFG are due to a form of decision learning, termed response learning, that has been found to mediate repetition suppression effects when the same tasks are

used in both encoding and testing phases (Dobbins, Schnyer, Verfaellie, & Schacter, 2004), as these experiments had participants perform the size-judgment task for both encoding and testing phases (Koutstaal et al., 2001; Simons et al., 2003). Therefore, reductions in neuronal activity for different exemplars of objects observed in these experiments may not actually reflect priming of objects, per se, but are more likely a product of response learning.

Unexpectedly, however, visual similarity of exemplars pairs differentially affected priming magnitudes when assessed in the RFG. Most notably, further analyses of this finding revealed that priming magnitude for similar exemplar pairs was less than that of dissimilar exemplar pairs. In other words, the similar exemplar pairs led to an increase of activation, indicating exemplar-specific recognition; however, dissimilar exemplar pairs led to a decrease of activation, indicating exemplar-abstract recognition. Moreover, when visual similarity was assessed in the fusiform face area (FFA), the same effect was obtained. While at first these results seem confusing, as one might expect this area to mediate the specific recognition of objects, the interpretations and implications of these findings become clearer when evaluated in terms of shared characteristics between visually similar exemplar pairs and faces. Different exemplars of faces tend to be visually similar representations of "face" whereas different exemplars of houses tend to be visually dissimilar representations of "house". Accordingly, the results from this experiment reveal that activation patterns for faces did not differ from those of similar exemplar pairs, and activation patterns for houses did not differ from those of dissimilar pairs. Therefore, we interpret these findings to suggest that the RFG, and more

specifically the FFA, may be recruited for the disambiguation of visually similar exemplar pairs, such as faces.

While previous experiments assessing the FFA don't typically utilize a priming paradigm, the methodology can be thought of in terms of different exemplar priming. In these experiments, subjects view several unknown, or exemplars of, faces and houses, in which each consecutive stimulus is primed by its abstract visual representation. Increased activation in the FFA for faces as compared to houses could merely reflect the idea that bottom-up processing increases with greater the perceptual demands of disambiguating one visually similar object from the next. On the other hand, decreased activation for houses may be the result of conceptual priming in the absence of requiring bottom-up processes for disambiguation (see Bar et al., 2006 for a similar idea). However, it should be noted that this finding and explanation for RFG and FFA sensitivity to visual similarity diverges from both the RBC model of object recognition and previous experiments evaluating different exemplar priming. First, the RBC model would predict that similar, but not dissimilar, exemplar pairs would prime one another due to the fact that similar pairs share many basic components. Moreover, a previous neuroimaging experiment suggests the fusiform cortex represents geon, and not abstract visual, information (Hayworth & Biederman, 2006). Lastly, a divided visual field study found exemplar abstract priming when visually similar, but not visually dissimilar, forms were presented to the right hemisphere (Marsolek, 2004). Although the findings from the present experiment implicate the role of the FFA in processing more than just faces and/or objects of perceptual expertise, these results are in need of further assessment, as they contradict predictions based on previous experiments. Therefore, in attempts to

replicate these findings, we conducted a second experiment designed to specifically test visual similarity, as this variable was not manipulated in the first experiment.

Experiment 2

The first experiment found an effect of exemplar pair similarity in the right fusiform gyrus (RFG), including the fusiform face area (FFA), revealing that this area is sensitive to visual similarity of different exemplars with a common name. Specifically, visually similar exemplar pairs exhibited greater activation than those that were rated as dissimilar in both the RFG and localized FFA, suggesting that this area mediates abstract recognition of objects when an exemplar is visually dissimilar from its corresponding exemplar. These findings also suggest that the FFA is not just a face area, but also an area that processes any visually similar exemplars of the same object name to a greater extent than those that are visually dissimilar. Experiments suggesting the role of a domain-specific "face area" (Kanwisher et al., 1997; McCarthy et al., 1997; Kanwisher et al., 1998; Yovel & Kanwisher, 2004; Loffler et al., 2005) could reflect this idea in that faces are visually similar whereas houses are not. A neuroimaging study examining the patterns of activation for a mean, or prototypical, face compared with faces that deviated from the mean on a continuum, found that faces around the mean resulted in greater FFA activation that those that were farthest from the mean (Loffler et al., 2005). In line with our findings, these results suggest that FFA activation increased when faces were visually similar (around the mean), but decreased when they were dissimilar.

While these unexpected findings seem to provide compelling evidence that the RFG responds differently to visually similar and dissimilar exemplars, the direction of these differences contradict both models and previous findings of visual similarity effects

on object recognition. In particular, RBC model of object recognition posits that object recognition is achieved through the perception of basic components termed geons, which are then arranged and matched onto representations stored in memory (Biederman, 1987; Hummel & Biederman, 1992). Abstract recognition of different exemplars of objects requires that the geon structural configuration is similar across exemplars (Biederman, 1987). Thus, this model would predict that visually similar exemplars, consisting of analogous geon structural configurations, would prime one another, but visually dissimilar exemplars would not. In line with this prediction, a divided visual field study investigating visual similarity effects on letter-case priming found that letter strings with visually similar upper and lower case forms demonstrated abstract recognition when presented to the right hemisphere; however, priming was not observed for visually dissimilar upper and lower case letter forms (Marsolek, 2004). Therefore, it is surprising that Experiment 1 demonstrated an opposite effect of similarity such that the RFG and FFA mediated priming for visually dissimilar, but not similar, exemplar pairs.

Although the results from Experiment 1 diverge from what might be predicted, the findings of FFA differential activation for visually similar and dissimilar exemplar pairs may provide an explanation. The first experiment demonstrated that the activation for faces and similar exemplar pairs did not differ, and the activation for houses and dissimilar exemplar pairs did not differ, suggesting that faces and houses fall into the classification of similar and dissimilar exemplars, respectively. Therefore, the FFA may not be a domain-specific area mediating the recognition of faces, but instead a process-specific area that is recruited for discriminating between visually similar exemplars, a process required for specific object recognition. While process-specific accounts of FFA

activation have focused on the idea that this area mediates recognition of objects with which one has perceptual expertise, these findings could also be interpreted in terms of visual similarity, as the experts performing the task viewed different exemplars of the same object (i.e. birds), which happened to be visually similar to one another (Gauthier et al., 2000).

The aim of this study is to directly test the hypothesis that the FFA processes visually similar exemplars of any object class to a greater extent than those that are visually dissimilar. Since the basis for defining similar and dissimilar exemplar pairs in the first experiment relied on ratings that subsequently split the exemplar pairs into the two corresponding groups, it is important that the effects of similarity be directly manipulated to further test this hypothesis. Accordingly, this experiment only looked at priming effects in the FFA, as this is a strong test of the process-specific hypothesis. Within the localized FFA region, this experiment examines neural correlates associated with repetition of the same object, a visually similar different exemplar of an object, or a visually dissimilar exemplar of an object, as compared to that of novel, or unrepeated objects. If priming is observed in the FFA for visually dissimilar exemplar pairs, but not visually similar exemplar pairs, it would suggest that these areas are sensitive to visual similarity and thus process visually similar exemplars to a greater extent than those that are visually dissimilar. In line with this argument, it is expected that different exemplars of faces presented during the localizer task will demonstrate greater neuronal activity as compared to that observed with different exemplars of houses. Moreover, the activation patterns associated with faces and houses are expected to correspond with those for similar and dissimilar exemplar pairs, respectively, suggesting that these stimuli fall into

the analogous stimulus classifications. Therefore, if FFA activation for faces corresponds to that found with visually similar exemplar pairs, it would imply that greater FFA activation for faces does not reflect a face-specific processing area, but an area specialized for processing and disambiguating between visually similar exemplars of an object.

Method

Design.

A one-way repeated measures design was utilized for this experiment, in which prime type (unprimed vs. same vs. different exemplar similar vs. different exemplar dissimilar) is the within subjects variable.

Subjects.

Twenty-two volunteers from Rice University, Baylor College of Medicine, and the University of Texas Medical School (11 male; mean age 21) participated in the neuroimaging study. All subjects completed a screening questionnaire to ensure they did not have a history of neurological or psychiatric problems. Moreover, subjects were all right-handed, and had normal, or corrected-to-normal vision. Informed consent within the guidelines set forth and permitted by the Institutional Review Board at Rice University was received from each subject. Subjects were paid for their participation.

Materials.

Stimuli includes some of the exemplar pairs from the first experiment, in addition to either a visually similar or dissimilar exemplar pair, constituting a total of 40 objects for the purposes of collecting norming data. For each of the 40 objects, a similar and dissimilar exemplar was selected. Ten subjects participated in the normative behavioral

study. Subjects were native English speaking Rice University undergraduate and graduate students who either received course-credit in their psychology classes or payment for participating. Informed consent was obtained, and after completing the experiment, subjects received a debriefing form explaining the purpose of the experiment.

In the normative behavioral study, stimuli were presented on a computer screen and subjects were prompted to type in the name of the object. The trial advanced to the next object when the subject pressed the space bar, which signified a completed response. Exemplars were presented in a pseudorandom order that ensured different exemplars of the same object were spaced throughout the trial. Once subjects completed the naming task, they then rated exemplar pair visual similarity. For this task, pictures of each exemplar pair situated next to one another appeared above a rating scale of one, very dissimilar, to six, very similar. Subjects were instructed to rate the exemplar pairs based on how visually similar they appear by pressing the corresponding number keys on the keyboard. For these ratings, subjects were instructed to distribute their responses across all six points rather than always respond with a one or six.

Based on the naming and rating data, 36 of the 40 objects presented were selected for use in the fMRI experiment, comprising a total of 108 objects: a test item with both a similar and dissimilar exemplar. All exemplars of an object obtained at least 85% name agreement, and the mean similarity rating for similar exemplar pairs (4.87) is greater than that for dissimilar exemplar pairs (3.18), $t(35) = 18.07, P < .0001$. For an example of a test object and its corresponding visually similar and dissimilar exemplar, refer to Figure 13. The presentation of objects was counterbalanced on measures of similarity. This

experiment also included 36 nonobjects, 30 faces, and 30 houses. Thirty of the nonobjects are the same as those used in Experiment 1, and six more were selected from the same stimuli set (Burgund, 2000) in order to have an equal number of objects and nonobjects. In addition to the 26 houses (http://www.turbosquid.com/) from Experiment 1, four more images of houses were selected in order to obtain a total of 30. The proposed experiment also used seven Caucasian female faces from Experiment 1; however, in order to maximize similarity among faces, 23 more faces of the same sex and race were selected from the same database (http://www.tarrlab.org/).

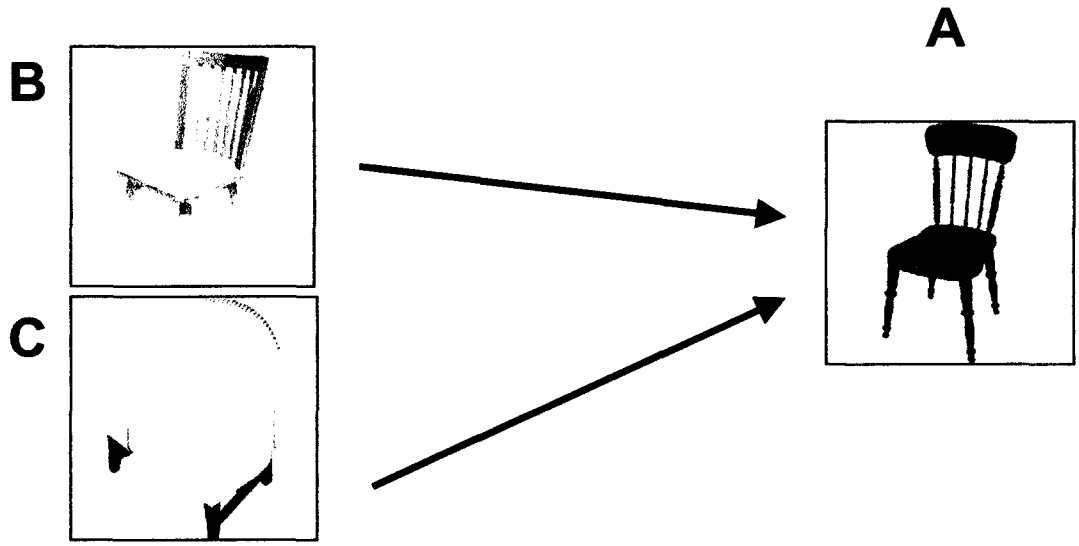

Figure 13. Example of a test object (A) with its corresponding visually similar (B) and visually dissimilar (C) exemplar pair. For each test object, subjects saw either the visually similar or visually dissimilar exemplar during the encoding phase.

All images were presented centrally, in grayscale against a white background, and subtended approximately 2° x 2° of visual angle. Presentations, response-time measurement, object naming data, and similarity ratings were controlled by the PsyScope software package (Cohen et al., 1993).

Procedure.

The procedure of the fMRI experiment was the same as that in the first experiment with two exceptions. First, subjects only performed the object-decision task during the test phase, since the previous experiment did not find task effects. Second, instead of including different viewpoint prime types, this experiment included different exemplars that are either visually similar or dissimilar to the target exemplar. The objects were split in half so that for each object, subjects saw either the similar or dissimilar exemplar during the encoding phase where the test object remains constant for all subjects.

Subjects completed two runs of the encoding task and two runs of the testing task. The encoding task is the same as Experiment 1, and thereafter, subjects performed the object-decision task during the test phase. The presentation of objects was administered in different counterbalanced orders. In each trial, no more than three runs of the same prime type (unprimed vs. same vs. different exemplar similar vs. different exemplar dissimilar) or stimulus type (object vs. nonobject) appeared consecutively. Immediately following the test phase, subjects completed the same localizer task as used in Experiment 1. No more than three faces or houses appeared consecutively during the localizer task. The approximate length of each run was five minutes for encoding, four minutes during testing, and three minutes for the localizer.

Image Acquisition.

These parameters were the same as those in Experiment 1.

Image Analysis.

Data from each subject were preprocessed in the same manner as that in Experiment 1. Likewise, preprocessed data were analyzed using the General Linear Model (GLM; Friston et al., 1994; Josephs et al., 1997; Miezen et al., 2000; Zarahn et al., 1997) in the FIDL analysis package (http://www.nil.wustl.edu/~fidl), as in Experiment 1. Neural signals for the four conditions of interest [prime (4)] to assess priming effects and for the two conditions of interest [faces vs. houses] to localize the FFA were modeled in the GLM across the seven time points (i.e., image acquisitions), beginning immediately after stimulus onset. The procedure for modeling the conditions in the GLM was identical to that of Experiment 1 with the one exception that the number and type of conditions modeled were different (see Experiment 1 *Image Analysis* section for reference).

Regions of interest localizing the FFA were defined based on a voxel-wise analysis, in which a two-way repeated-measures ANOVA where time (at the seven time points) and stimulus type (face vs. house) were the independent variables. The statistical image was smoothed with a 3-mm radius hard sphere kernel, and then masked by an additional image reflecting voxels in which the percent signal change of the bold signal from baseline differed for faces compared with houses. A peak (local extremum) search algorithm was used to identify the coordinates (Talairach & Tournoux, 1988) of activation peaks ($P < .01$, uncorrected) in the masked images. Thereafter, coordinate averaging combined peaks separated by less than 10-mm, and spheres (10-mm radius) were centered on each peak. Lastly, masks were placed on the spherical images to exclude voxels that did not reach a statistical threshold of $P < .05$ (uncorrected).

Region-based analyses were conducted on the area defined in the voxel-wise analysis. The FFA was localized using a two-way, repeated measures ANOVA in which time (at the seven time points) and stimulus type (face vs. house) were the independent variables.

Results

FFA Localizer.

One RFG region emerged from the voxel-wise analysis designed to anatomically localize the FFA. Most importantly, this region was centered on coordinates in stereotactic space (41, -61, -18 [Figure 14A]; Talairach & Tournoux, 1988) that was in close proximity to the FFA region of interest obtained in Experiment 1 (41, -55, -15). A region-based analysis revealed that this area shows greater peak activation for faces (.51) than houses (.30), $t(21) = 3.23$, $P < .005$ (see Figure 14B), which is characteristic of FFA activity.

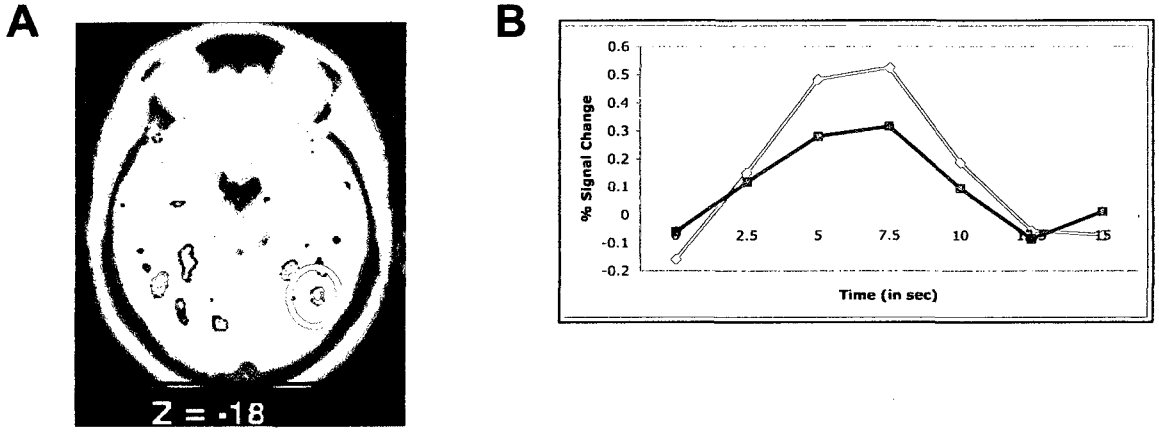

Figure 14. Region within the RFG localized as the FFA (A [41, -62, -18]) exhibiting greater activation for faces, shown in red, as compared to houses, shown in blue (B).

Analysis of objects in the FFA shows a trend for object priming such that the peak activation for same primed objects (.39) was less than that for unprimed objects (.52),

$t(21) = 1.68, P < .11$; however, the results do not suggest that the FFA responds differently to the similarity of exemplar pairs. That is, similar exemplar pairs (.39) did not differ from that of same primed (.39) or unprimed (.52) objects, $t(21) = .02, P = .98$ and $t(21) = 1.50, P = .15$. Moreover, dissimilar exemplar pairs (.44) did not differ from that of same primed (.39) and unprimed (.52) objects, $t(21) = 1.12, P < .28$ and $t(21) = .90, P < .38$. Likewise, the difference between similar exemplar pairs (.39) and dissimilar exemplar pairs (.44) was not significant, $t(21) = 1.08, P < .29$ (Figure 15). To further determine whether or not faces and houses can be considered similar and dissimilar exemplars, respectively, analyses were performed comparing activation patterns for these variables. The difference between the peak activation for faces (.51) and similar exemplar pairs (.39) approached significance, $t(21) = 1.75, P < .10$; whereas the difference between the peak activation for houses (.30) and dissimilar exemplar pairs was significant, $t(21) = 2.35, P < .05$. Therefore, it appears as though faces and houses were not processed in the same manner as the aforementioned classifications described above.

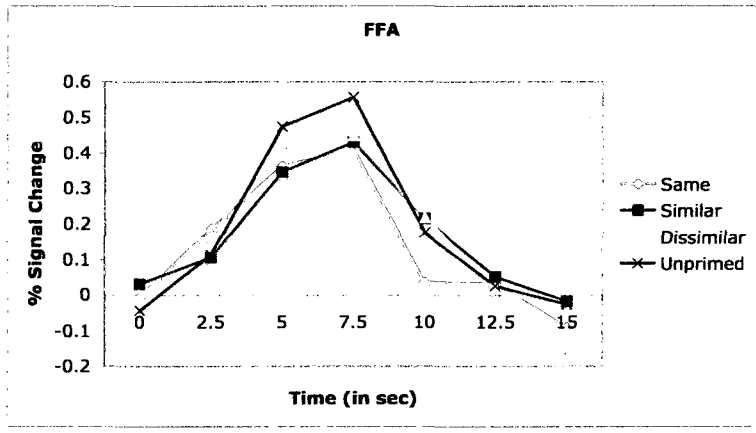

Figure 15. FFA activation patterns for the four prime types demonstrating no significant differences between visually similar and visually dissimilar exemplar pairs.

Discussion

This experiment attempted to explain the findings of visual similarity effects obtained in Experiment 1 by directly manipulating visual similarity of objects. Previous research debates the issue of whether or not the FFA is a face-specific area (Kanwisher et al., 1997; McCarthy et al., 1997; Kanwisher et al., 1998; Yovel & Kanwisher, 2004; Loffler et al., 2005) or a processes-specific area developed through perceptual expertise with one class of objects (Tarr & Gauthier, 2000; Gauthier et al., 1997; Gauthier et al., 1999; Gauthier et al., 2000; Gauthier et al., 2000). The results from Experiment 1 suggest that this area is process-specific in that it mediates specific recognition for objects that are visually similar. We hypothesized that the FFA may process visually similar exemplars to a greater extent than those that are visually dissimilar in order to disambiguate one exemplar from another. However, the results from the present experiment imply that this is not the case. That is, the activation patterns associated with visually similar and visually dissimilar exemplar pairs did not differ. Furthermore, the activation for faces differed from that of similar exemplar pairs, whereas the activation for houses differed from that of dissimilar exemplar pairs, implying that faces and houses were not processed in an analogous manner to that of similar and dissimilar exemplars, respectively.

The finding that FFA activation was not sensitive to variations in the visual similarity of exemplar pairs is in line with both the RBC model of object recognition (Biederman, 1987; Hummel & Biederman, 1992) and previous findings of similarity effects (Marsolek, 2004). Thus, it is possible that the visual similarity effects obtained in the first experiment reflect a methodological problem in the way that similarity was

defined. As previously noted, effects of visual similarity were assessed by splitting the exemplar pairs into two groups based on the similarity ratings obtained from the norming study. However, the stronger test of visual similarity effects used in the present experiment provides evidence that this factor does not differentially affect priming in the fusiform cortex.

General Discussion

In these experiments, we examine possible explanations for why previous research (Koutstaal et al., 2001; Vuilleumier et al., 2002; Simons et al., 2003) provides mixed support for the dissociable subsystems theory of object recognition. While the role of a specific visual form (SVF) subsystem consistently demonstrates that it operates more effectively in the right hemisphere, support for the role of an abstract visual form (AVF) subsystem operating more effectively in the left hemisphere is unclear. That is, the dissociable subsystems theory suggests that the left hemisphere supports both viewpoint and exemplar abstract recognition (Marsolek, 1999; Burgund & Marsolek, 2000; Burgund, 2000), but neuroimaging experiments reveal divergent findings in regards to abstract recognition of different exemplars in the left hemisphere (Vuilluemier et al., 2002; Koutstaal et al., 2001; Simons et al., 2003). In particular, some experiments demonstrate exemplar abstract recognition in the LFG (Koutstaal et al., 2001; Simons et al., 2003), while another implicates this region in the recognition of specific exemplars (Vuilleumier et al., 2002). In Experiment 1, we investigated the possible effects of task and visual similarity on exemplar abstract recognition, as both the processing demands of the task and the overlap of basic visual components across exemplars could affect the magnitude of priming; however, the results revealed that the LFG mediates viewpoint,

but not exemplar, abstract recognition, and neither task nor visual similarity differentially affected LFG activation. Conversely, the RFG, including the fusiform face area (FFA), demonstrated an effect of visual similarity such that specific recognition was observed for similar exemplar pairs, yet abstract recognition was observed for dissimilar exemplar pairs. When compared with activation for faces and houses in the FFA, neural responses for similar exemplars were analogous to that for faces and activation patterns for dissimilar exemplar pairs were analogous to that for houses. In Experiment 2, we tested the hypothesis that the FFA is a process-specific area that is recruited when the perceptual demands of disambiguating one similar exemplar from another are high. This experiment used a more stringent measure of visual similarity from that used in Experiment 1, and did not find an effect of visual similarity in the FFA, suggesting that the results from Experiment 1 were due to an issue in how visual similarity was defined.

In both Experiments 1 and 2, findings reveal that a SVF subsystem operates more effectively in the right hemisphere, in which the RFG is recruited for this process. Yet, in contrast to some studies (Marsolek, 1995, 1999, 2004), the findings reveal that an AVF subsystem mediated by the LFG is involved in abstract recognition of different viewpoints of an object, but not for different exemplars of an object. Although these findings contradict those found in some neuroimaging experiments (Koutstaal et al., 2001; Simons et al., 2003), they support results assessing the recognition-by-components (RBC) model of object recognition (Biederman & Cooper, 1991; Biederman & Gerhardstein, 1993; Hayworth & Biederman, 2006). In particular, the RBC model of object recognition suggests that abstract recognition of different viewpoints of an object is achieved through different processes than that for exemplar abstract recognition. That

is, viewpoint abstract recognition represents visual priming based on geon matching from one viewpoint to another; on the other hand, exemplar abstract recognition represents abstract visual form priming based on nonvisual properties of objects belonging to the same class with a common name. Critically, an fMRI study provides evidence that the fusiform cortex represents geons of objects, but does not represent conceptual information (Hayworth & Biederman, 2006). To this end, it appears as though the fusiform cortex mediates viewpoint, but not exemplar, abstract recognition, which is in line with the findings from the current experiments. This, however, does not necessarily refute the dissociable subsystems theory; it merely suggests that AVF subsystems that operate more efficiently in the left hemisphere may be localized in different regions of the brain. While the AVF subsystem recruited for viewpoint abstract recognition is located in the LFG, it's possible that a different left hemisphere region is involved in exemplar abstract recognition. In line with this idea, a number of studies demonstrate that regions within the prefrontal cortex respond to different exemplars of an object (Freedman, Riesenbuer, Poggio, & Miller, 2002; Freedman, Riesenhuber, Poggio, & Miller, 2003), which is thought to signify lexico-semantic processing (Vuilleumier et al., 2002; Buckner, Koutstaal, Schacter, & Rosen, 2000; Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000).

Taken together, these findings highlight the shortcomings of both the RBC model and dissociable subsystems theory of object recognition. That is, neither explanation provides an explicit description of how a visual input form can be both specifically identified as a particular object while also abstractly recognized as being the same object from a different view or as belonging to a class of objects that share a common name.

While the RBC model can account for viewpoint invariance, it lacks a neuroanatomically feasible explanation for the parallel nature of both specific and abstract visual form processes, as this model assumes a single system for object recognition. The dissociable subsystems theory solves this problem by demonstrating that there are hemispheric asymmetries in the two types of processes, but this theory falls short in that it cannot account for separable neural networks that have been found in the present experiments and previous experiments (Vuilleumier et al., 2002; Hayworth & Biederman, 2006) to underlie the abstract recognition of viewpoints as compared with that of exemplars. Thus, a full account of specific and abstract object recognition that describes both the processes for recognizing a different viewpoint of an object compared with a different exemplar of an object class and the neural networks implicated in such tasks is in need. In order to understand the neuronal processes involved, we turn to a computational model proposed by Riesenhuber and Poggio (1999, 2000, 2002) that provides a plausible explanation for the findings from our experiments and others (Vuilleumier et al., 2002; Hayworth & Biederman, 2006). We will begin first with a brief description of the computational model, and then discuss how this model can be extended to encompass data from several object recognition experiments discussed previously in this paper (Vuillleumier et al., 2002; Hayworth & Biederman, 2006; Burgund & Maroslek, 2000; Marsolek, 1999; Burgund, 2000; Biederman & Cooper, 1991; Biederman & Gerhardstein, 1993; Koutstaal et al., 2001; Simons et al., 2003; Kanwisher et al., 1997; McCarthy et al., 1997; Kanwisher et al., 1998; Yovel & Kanwisher, 2004; Loffler et al., 2005; Tarr & Gauthier, 2000; Gauthier et al., 1997; Gauthier et al., 1999; Gauthier et al., 2000; Gauthier et al., 2000).

Single cell recordings of primates have led to the development of a computational model (Riesenhuber & Poggio, 1999, 2000, 2002) that helps to describe the neurological underpinnings of object recognition. This model assumes a simple, feed-forward, hierarchical structure, in which the cells in early visual areas project information to later areas in the ventral stream. The cells in V1 are known to have small receptive fields and respond to simple bar like structures. As one proceeds through the ventral stream, the receptive fields become increasingly larger, and respond to more complex stimuli, such as faces (Tanaka, 1996; Logothetis & Sheinberg, 1996; Perrett, Hietanen, Oram, & Benson, 1992; Logothetis, Pauls, & Poggio, 1995). Due to the neuroanatomical properties of the cells in the ventral stream, the model makes explicit assumptions as to how areas from V1 to the lateral occipital complex (LOC) respond to visual stimuli and how the information garnered in these areas is sent to the prefrontal cortex to perform tasks such as categorization.

In their computation model, Riesenhuber and Poggio (1999, 2000, 2002) propose that the ventral stream is made up of simple cells that respond to specific properties of an object, such as line orientation, and complex cells that represent view-tuned and view-invariant information. The simple cells are located in areas V1 through V4, in which each successive region pools the information from the preceding region in order to represent more complex properties of the whole object. V4 then projects information to the LOC, which contains view-tuned and view-invariant cells (Logothetis et al., 1995). The view-tuned cells, which are mostly located in posterior portions of the LOC, pool the information received by V4, and respond only to the particular view of an object. The view-tuned cells project afferents to anterior regions of the LOC, also known as the

fusiform cortex, which are then pooled together to match neurons that represent the whole object, or those neurons that are view-invariant. Tasks such as categorization are performed by circuits located in the prefrontal cortex (Freedman et al., 2002; Freedman et al., 2003), which receive inputs from the view-invariant cells (Riesenhuber & Poggio, 1999, 2000, 2002). By this account, the anterior portions of the LOC mediate recognizing an object from a different viewpoint, and the prefrontal cortex mediates the recognition for different exemplars of an object.

Riesenhuber and Poggio's (1999, 2000, 2002) computational model provides not only a good framework for explaining the neuronal processes by which object recognition is achieved, but also addresses the shortcomings of previous theories (Biederman, 1987; Hummel & Biederman, 1992; Marsolek, 1999; Burgund & Marsolek, 2000). That is, the predictions from this model are in line with data suggesting that the fusiform cortex represents object shape information, but not object category membership information (Vuilleumier et al., 2002; Hayworth & Biederman, 2006). While these predictions are in line with an fMRI study assessing the RBC model of object recognition (Hayworth & Biederman, 2006), the computational model expands on this idea by providing an explicit account of how the LOC mediates both specific and viewpoint abstract object recognition. The key feature here is that the LOC contains both view-tuned and view-invariant cells (Riesenhuber & Poggio, 1999, 2000, 2002; Logothetis et al., 1995), which helps to explain how the specific identification of an object and the abstract recognition of that object from a different viewpoint operate in parallel. Moreover, the computational model confirms behavioral studies assessing the RBC model that suggest abstract recognition for exemplars of an object class is achieved by different processes than that

for viewpoints of the same object (Biederman & Cooper, 1991; Biederman & Gerhardstein, 1993). That is, Riesenhuber and Poggio (1999, 2000, 2002) propose that the prefrontal cortex retrieves information about the visual properties of an object from the LOC in order to make judgments of subordinate and superordinate category membership. Therefore, recognizing the same object at different viewpoints is performed at earlier stages in the ventral stream and relies primarily on visual properties retrieved from each view. In contrast, recognizing an object as belonging to a class of objects occurs at later stages of visual form processing, and relies primarily on lexico-semantic processes. This aspect of the model (Riesenhuber & Poggio, 1999, 2000, 2002) also addresses the problem encountered with the dissociable subsystems theory in that it differentiates between the neural networks involved in abstract viewpoint and abstract exemplar recognition. However, one limitation of the computational model proposed by Riesenhuber and Poggio (1999, 2000, 2002) is that it does not make any explicit claims about hemispheric asymmetries thought to be involved in specific and abstract object recognition.

Although Riesenhuber and Poggio (2000) do not address the issue of hemispheric asymmetries in terms of the types of cells located in the right versus left LOC, it is important to extend their model to include this factor, as it has been demonstrated consistently in the literature (Marolek, 1999; Burgund & Marsolek, 2000; Burgund, 2000; Marsolek, 2004; Koutstaal et al., 2001; Vuilleumier et al., 2002; Simons et al., 2003). To this end, it is expected that the ratio of view-invariant to view-tuned cells in the left anterior LOC is greater than that in the right anterior LOC. This extension of the model offers an explanation for why SVF subsystems are more effective in the right

hemisphere and AVF subsystems for recognizing different viewpoints of an object are more effective in the left hemisphere (Burgund & Marsolek, 2000; Burgund, 2000). Together the computational model (Riesenhuber & Poggio, 1999, 2000, 2002) and the proposed extension provide a reasonable explanation for the findings from the current experiments, while also addressing the shortcomings of both the RBC model and dissociable subsystems theory of object recognition.

Additionally, the proposition that the right anterior LOC contains a greater number of view-tuned than view-invariant cells can also account for the finding that an area located within the RFG, the FFA, responds preferentially to faces (Kanwisher et al., 1997; McCarthy et al., 1997; Kanwisher et al., 1998; Yovel & Kanwisher, 2004; Loffler et al., 2005) and classes of objects with which one has perceptual expertise (Tarr & Gauthier, 2000; Gauthier et al., 1997; Gauthier et al., 1999; Gauthier et al., 2000; Gauthier et al., 2000). Since view-tuned cells are sensitive to the specific orientation of an object, it could be assumed that these cells mediate holistic and configural processes thought to be involved in face and expert recognition, as these are the hallmarks of subordinate level processing. Moreover, the viewpoint sensitivity of large populations of view-tuned cells in the FFA would give rise to phenomenon such as the face inversion effect (Farah, Tanaka, & Drain, 1995; Freire, Lee, & Symons, 2000; Reed, Stone, Grubb, & McGoldrick, 2006) and inversion effects found in dog experts when recognizing pictures of dogs (Diamond & Carey, 1986). Thus, the inclusion of a distinction between the ratio of view-tuned to view-invariant cells in the right versus left anterior LOC is essential in order to explain FFA activity as well.

In conclusion, the LOC represents view-dependent and view-invariant object information. Simple cells in early visual areas respond to specific features of an object, such as line orientation. The LOC pools the information from simple cells, and the view-tuned and view-invariant cells located within the LOC support the specific identification of an object and the abstract recognition of that object from a different viewpoint. In order to account for hemispheric asymmetries, we propose that the RFG is mostly made up of view-tuned cells which mediate the specific recognition of both objects and faces, while the LFG contains a greater number of view-invariant cells which give rise to the abstract recognition of an object when presented at different viewpoints. While the LOC is recruited for the identification of a specific object and the abstract recognition of that object from a different viewpoint, the prefrontal cortex mediates abstract recognition for different exemplars of an object. The view-invariant cells located within the LFG send signals to the prefrontal cortex, in which the classification of an object based on subordinate or superordinate levels is achieved. Thus, exemplar abstract object recognition recruits frontal regions involved in lexico-semantic processes, but viewpoint abstract recognition can be performed at earlier stages of visual input processing that recruit the anterior regions of the left LOC known as the left fusiform cortex. Because the model focuses on bottom-up processes, it is still a question as to how top-down influences, such as response learning (Dobbins et al., 2004) affect object recognition and LFG activation. Riesenhuber and Poggio (1999, 2000, 2002) speculate that task learning may affect LOC activation, but do not actually model these processes. Future research is needed to assess the effect of task learning of fusiform activity in order to address the potential confound in previous experiments demonstrating LFG mediation of exemplar

abstract object recognition (Koutstaal et al., 2001; Simons et al., 2003). It is possible that top-down effects of task learning affect the activation of the LFG, as this region is proposed to be involved in a network of object recognition processes that recruits areas for processing visual and lexico-semantic information.

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